

The referral of genera to particular tribes follows the classification of the Compositae in Heywood, Harborne, and Turner (1977). The sequence of tribes used within subfamilies is alphabetical, but tribal composition of each subfamily follows Bremer (1994), with recognition of tribe Tageteae, after Strother (1977). Chloroplast DNA and morphological cladistic analyses (e.g., Bremer, 1987; Jansen et al., 1992) are in reasonable agreement that the family should be divided into three subfamilies, Barnadesioideae, Asteroideae, and Cichorioideae. Most of the counts reported here come from Asteroideae.

#### ASTEROIDEAE

*Anthemideae.* Our count of  $n = 12$  for *Tanacetum cinerariaefolium* is very unusual, considering the constancy of  $x = 9$  throughout the genus. Heywood & Humphries (1977) also reported several very unusual chromosome numbers for *Tanacetum*, such as  $2n = 24, 34$ , and  $56$ , but no literature is cited as documentation.

*Astereae.* *Aster squamatus* has been counted previously as  $n = 10$  (Villa, 1978; Jansen & Stuessy, 1980; Dillon & Turner, 1982; Baltisberger, 1988). Our count of  $n = 5$  establishes what appears to be the diploid level within this species. Dillon & Turner (1982) distinguished this South American species from the closely related North American taxon, *A. subulatus* Michx., emphasizing differences in characters of the involucre. *Aster subulatus* has repeatedly been found to be diploid ( $n = 5$ ), except for one tetraploid count by Turner (1978) from Florida, and other reports of tetraploidy from Asia and Africa (Turner & Lewis, 1965; Matsuda, 1970; Miyagi, 1974). Our report of a new chromosome level for *A. squamatus*, therefore, suggests that it, too, has undergone infraspecific polyploidy, and that tetraploid cytodesmes have evolved independently within each taxon.

Of the 27 species of *Erigeron* found in South America (Solbrig, 1962), 10 species have been counted (*E. andicola* DC., *E. ecuadoriensis* Hieron., *E. fernandezianus* (Colla) Solbrig, *E. karwinskianus* DC., *E. lanceolatus* Wedd., *E. leptopetalus* Phil., *E. leptorhizon* DC., *E. maximus* (D. Don) DC., *E. myosotis* Pers., and *E. rupicola* Phil.). Our count of  $n = \text{ca. } 27$  for *E. apiculatus* is the first for the species and is at the hexaploid level. Another first count of  $n = 36\text{--}40$  for *E. pinnatus* is apparently at the octaploid level. *Erigeron karwinskianus*, a pantropical weed native to Mexico and Central America (Solbrig, 1962), has previously been counted as diploid, triploid ( $2n = 27$ ), tetraploid, and hex-

aploid from populations in Mexico and Central America. Our count from South America (Ecuador) is also tetraploid. However, there is also one diploid report from Ecuador for this species (Olsen, 1980). This is the only diploidy reported in the genus *Erigeron* from South America. An interesting observation is that hexaploids and octaploids predominate in South America, whereas diploids largely prevail in North America and Central America. This geographical partitioning between ploidy levels suggests that the genus may have originated in North America, which might be expected based on the greater number and diversity of species in that region.

Only one chromosome count has been reported previously for *Hinterhubera* (*H. imbricata*,  $n = 9$ ; Powell & Cuatrecasas, 1970), which comprises four species in the Andes. Our count of  $n = \text{ca. } 9$  for *H. lagesgui* is consistent with the basic number  $x = 9$  and is the first count for the species.

*Oritrophium*, a genus with 15 species mainly distributed in the Andes (Mabberly, 1987) and once treated as a section of *Erigeron* (Bentham & Hooker, 1873), has had, until now, only two chromosomally known species (*O. aciculifolium* Cuatrec.,  $n = 9$ , Turner et al., 1967 and *O. hirtopilosum* (Hieron.) Cuatrec.,  $n = 18$ , Dillon & Turner, 1982). Our new count of  $n = \text{ca. } 17$  for *O. venezuelense* is presumably also a tetraploid. The three closely related genera *Aster*, *Conyza*, and *Erigeron* have basic numbers of  $x = 9$ , which is consistent with the base found in *Oritrophium*.

*Eupatorieae.* *Ageratina* is composed of five subgenera and about 248 species and has very diverse chromosome numbers (King & Robinson, 1987). Although variations are known to exist within particular species comprising subgenus *Ageratina* (Grashoff et al., 1972; King et al., 1976), the basic number is likely  $x = 17$  (King & Robinson, 1987). Among our counts for three species belonging to subgenus *Ageratina*, two, *A. cuencana* ( $n = \text{ca. } 18$ ) and *A. rhyphodea* ( $n = \text{ca. } 18$ ), are reported for the first time. *Ageratina azangaroensis*, however, is counted as  $n = 12$  and  $n = 16\text{--}18$  from two different populations from Ecuador. Previously reported chromosome numbers for this species were  $n = 17$ , with or without one or more fragments (King et al., 1976). Whether our count of  $n = 12$  reflects an aberrant plant, a stabilized cytotype, or apomixis cannot be determined at this time. More sampling is needed.

*Chromolaena* has over 165 known species (King & Robinson, 1987); only 17 species have been counted (King & Robinson, 1970; King et al.,



Table 1. Chromosome counts of Compositae from Ecuador and Venezuela. First counts designated by \*\*; new chromosome level by \*.

Taxon	Gametic chromosome number <sup>a</sup>	Voucher <sup>b</sup>
ASTEROIDEAE		
ANTHEMIDEAE		
<i>Chrysanthemum parthenium</i> (L.) Bernh.	ca. 9	ECUADOR. Chimborazo: 6.8 km NE of Cajasamba, SN 5825.
<i>Cotula australis</i> (Less.) Hook. f.	9	ECUADOR. Loja: 50.6 km N of Loja, SN 5909.
** <i>Tanacetum cinerariaefolium</i> Sch. Bip.	12	ECUADOR. Tungurahua: 21.9 km N of Riobamba, SN 5941.
ASTEREAE		
*Aster squamatus (Spreng.) Hieron.	5	ECUADOR. Cañar: 7.7 km N of Cañar SN 5787.
<i>Baccharis latifolia</i> (Ruiz & Pav.) Pers.	18	ECUADOR. Pichincha: 2.2 km N of Tambillo, SN 5787.
<i>Blakiella bartsiiifolia</i> (S. F. Blake) Cuatrec.	9	VENEZUELA. Mérida: Páramo Piedras Blancas, BG 3959
** <i>Erigeron apiculatus</i> Benth.	ca. 27	ECUADOR. Tungurahua: 21.9 km N of Riobamba, SN 5943.
<i>Erigeron karwinskianus</i> DC.	ca. 18	ECUADOR. Azuay: 20.9 km S of Cuenca, SN 5925.
** <i>Erigeron pinnatus</i> Turcz.	36–40	ECUADOR. Chimborazo: 6.8 km NE of Cajasamba, SN 5824.
<i>Hinterhubera imbricata</i> Cuatrec. & Aristeg.	9	VENEZUELA. Mérida: Páramo Piedras Blancas, BG 3886.
	ca. 10	VENEZUELA. Mérida: Páramo Piedras Blancas, BG 3954.
** <i>Hinterhubera lagesgui</i> Wedd.	ca. 9	VENEZUELA. Mérida: Páramo Piedras Blancas, BG 3953.
** <i>Oritrophium venezuelense</i> (Steyerm.) Cuatrec.	ca. 17	VENEZUELA. Mérida: Páramo Piedras Blancas, BG 3873.
EUPATORIEAE		
<i>Ageratina azangaroensis</i> (Sch. Bip. ex Wedd.) R. M. King & H. Rob.	12	ECUADOR. Chimborazo: 15.0 km SW of Cajasamba, SN 5837.
	16–18	ECUADOR. Cotopaxi: 16.2 km S of Machachi, SN 5952.
** <i>Ageratina cuencana</i> (B. L. Rob.) R. M. King & H. Rob.	ca. 18	ECUADOR. Tungurahua: along path from W end of Baños to Chaupi, SN 5800.
<i>Ageratina exerto-venosa</i> (Klatt) R. M. King & H. Rob.	36–40	ECUADOR. Loja: 21.4 km NNW of Saraguro, SN 5921.
** <i>Ageratina rhyphodea</i> (B. L. Rob.) R. M. King & H. Rob.	ca. 18	ECUADOR. Loja: 13.9 km NE of Saraguro, SN 5916
** <i>Chromolaena leptcephala</i> (DC.) R. M. King & H. Rob.	9	ECUADOR. Tungurahua: on path from W end of Baños to Chaupi, SN 5804.
<i>Oxylobus glanduliferus</i> (Sch. Bip.) A. Gray	16	VENEZUELA. Mérida: Páramo Piedras Blancas, BG 3879.
HELIANTHEAE		
<i>Ambrosia peruviana</i> Willd.	18	ECUADOR. El Oro: 1.8 km N of El Cambio, SN 5859.
** <i>Coespeletia timotensis</i> (Cuatrec.) Cuatrec.	19	VENEZUELA. Mérida: Páramo Piedras Blancas, BG 3966.
	19	VENEZUELA. Mérida: Páramo Piedras Blancas, BG 3883.
** <i>Espeletia batata</i> Cuatrec.	19	VENEZUELA. Mérida: Páramo Piedras Blancas, BG 3874.



Table 1. Continued.

Taxon	Gametic chromosome number <sup>a</sup>	Voucher <sup>b</sup>
<i>Garcilassa rivularis</i> Poepp. & Endl.	ca. 16	ECUADOR. Chimborazo: NW edge of Bucay, SN 5854.
<i>Monactis flaverioides</i> H.B.K.	30–32	ECUADOR. Pichincha: 2.2 km N of Tambillo, SN 5786.
	ca. 30	ECUADOR. Tungurahua: 38.4 km N of center of Riobamba, SN 5945.
** <i>Ruilopezia floccosa</i> (Standl.) Cuatrec.	19	VENEZUELA. Mérida: Páramo Piedras Blancas, BG 3965.
<i>Sigesbeckia jorullensis</i> H.B.K.	ca. 16	ECUADOR. Loja: 50.6 km N of Loja, SN 5911.
<i>Steiractina mollis</i> S. F. Blake	14	ECUADOR. Cañar: 6.7 km S of Suscal, SN 5931.
** <i>Vasquezia titicacensis</i> (Meyen & Walp.) S. F. Blake	20	ECUADOR. Cañar: 3.3 km N of Cañar, SN 5927.
INULEAE		
<i>Gamochaeta americana</i> (Mill.) Wedd.	14	VENEZUELA. Mérida: Páramo Piedras Blancas, BG 3920.
** <i>Stuckertiella capitata</i> (Wedd.) Beauverd	11–12	ECUADOR. Chimborazo: 10.5 km S of Cajabamba, SN 5830.
SENECIONEAE		
** <i>Gynoxys buxifolia</i> Cass.	ca. 36	ECUADOR. Chimborazo: 15.0 km SW of Cajabamba, SN 5838.
	ca. 12	ECUADOR. Cotopaxi: 12.6 km S of Machachi, SN 5951.
** <i>Pentacalia sclerosa</i> (Cuatrec.) Cuatrec.	ca. 20	VENEZUELA. Mérida: Páramo Piedras Blancas, BG 3906.
<i>Senecio formosus</i> H.B.K.	40	VENEZUELA. Mérida: Páramo Piedras Blancas, BG 3870.
** <i>Senecio teretifolius</i> (H.B.K.) DC.	20	ECUADOR. Chimborazo: 8.6 km NW of center of Riobamba, SN 5938.
TAGETEAE		
<i>Tagetes zypaquirensis</i> Humb. & Bonpl.	ca. 12	ECUADOR. Chimborazo: 9.7 km NW of center of Riobamba, SN 5940.
CICHORIOIDEAE		
LIABEAE		
<i>Liabum floribundum</i> Less.	18	ECUADOR. Chimborazo: 44.4 km SW of Cajabamba, SN 5845.
* <i>Erato sodiroi</i> (Hieron.) H. Rob.	9	ECUADOR. Chimborazo: 34.1 km N of jct. rd. to Huigra, SN 5934.
MUTISIEAE		
<i>Onoseris albicans</i> (D. Don) Ferreyra	18	ECUADOR. Azuay: 54.2 km NNE of Saraguro, SN 5923.
<i>Perezia multiflora</i> (Humb. & Bonpl.) Less.	8	ECUADOR. Chimborazo: 10.5 km S of Cajabamba, SN 5827.

<sup>a</sup> Numbers represent bivalents.  
<sup>b</sup> Ecuadorian collections by *Stuessy & Nesom* (SN); Venezuelan collections by *Berry & Gómez* (BG).

1976; Mathew & Mathew, 1983; Strother, 1983; Baker & Parfitt, 1986; Bernardello, 1986; Sundberg et al., 1986). Most previous reports suggest that the basic number of this genus is  $x = 10$ , although some variations have been found due to irregular meiosis (for *C. laevigata* (Lam.) R. M. King & H. Rob.,  $2n = \text{ca. } 56\text{I}$ , Sundberg et al., 1986; for *C. odorata* (L.) R. M. King & H. Rob.,  $2n = 58$ , Ghosh, 1961,  $n = \text{ca. } 31 + 4\text{I}$ , King et al., 1976). Our count of  $n = 9$  with clear bivalents



for *C. leptcephala* suggests that it is an aneuploid within the genus.

*Heliantheae.* *Coespeletia* (Espeletiinae), with eight species once included in *Espeletia* (Smith & Koch, 1935) but separated by Cuatrecasas (1976), has two chromosomally known species with  $n = 19$  (*C. moritziana* (Sch.Bip. ex Wedd.) Cuatrec., *C. thyrsiformis* (Smith) Cuatrec.; Powell & Cuatrecasas, 1975). Our new counts of  $n = 19$  for two individuals of *C. timotensis* (Cuatrec.) Cuatrec. are consistent with these reports. Another generic segregate, *Ruilopezia*, is known to have  $n = 19$  in *R. bromelioides* (Cuatrec.) Cuatrec. (Powell & Powell, 1978) and  $n = 19$  in a possible intergeneric hybrid between *R. floccosa* and *Espeletiopsis pannosa* (Standley) Cuatrec. (Powell & Cuatrecasas 1970; cited as *Espeletia floccosa*  $\times$  *Espeletia pannosa*). Our count of  $n = 19$  is the first for *R. floccosa*. In addition, *Espeletia batata* has been newly counted as  $n = 19$ . The counts for these species are consistent with the rest of Espeletiinae, which contains seven genera that include species previously placed in *Espeletia* Mutis ex Humb. & Bonpl. (Cuatrecasas, 1976). More than 50 species have been counted, all as  $n = 19$  (Powell & King, 1969; Powell & Cuatrecasas, 1970, 1975). Despite the obvious morphological differences among these newly created genera, they appear to represent a monophyletic unit. The putative hybrid between two of these genera underscores their close affinity, as does the uniform chromosome number for all species of the subtribe counted to date. A more taxonomically meaningful approach might be to recognize sections and subgenera within a diverse single genus, *Espeletia*.

Our new count of  $n = 20$  for *Vasquezia titicacensis* is consistent with previous reports (*V. achillioides* (Less.) Less.,  $n = 9$ , Olsen, 1980; *V. anemonifolia* (HBK) S. F. Blake,  $n = 19$ , Powell & King, 1969; Jansen et al., 1984; *V. oppositifolia* (Lag.) S. F. Blake,  $n = 20$ , Dillon & Turner, 1982). Dillon & Turner (1982) suggested that this genus has a basic number of  $x = 9$  or 10, in which case our report for *V. titicacensis* is also at the tetraploid level.

*Inuleae.* *Stuckertiella* is a genus with only two known species, both in S. America: *S. capitata* and *S. peregrina* Beauverd (Beauverd, 1913; Merxmüller et al., 1977). Our count of  $n = 11$ –12 for *S. capitata* is the first report for this genus. *Gamochoa* is the closest generic relative, itself sometimes treated as a section of *Gnaphalium* (Beauverd, 1913). The basic chromosome number of *Gnaphalium* sensu lato is suggested as  $x = 7$ , a

number which, along with  $x = 9$  and 10, is predominant in Inuleae (Merxmüller et al., 1977). Our count might be interpreted as coming from a descending aneuploid from  $n = 14$ , a number also occurring in the tribe (Merxmüller et al., 1977).

*Senecioneae.* *Gynoxys*, with about 100 species, has only three chromosomally known taxa (*G. fuliginosa* (HBK) Cass.,  $n =$  ca. 40, Hunziker et al., 1989; *G. parvifolia* Cuatrec.,  $n =$  ca. 40; and *G. tomentosissima* Cuatrec.,  $n = 40$  + fragment, Turner et al., 1967). The basic number of this genus has been suggested to be  $x = 10$  by Turner et al. (1967). Our new counts from two different populations in Ecuador for *G. buxifolia* are  $n =$  ca. 12 and  $n =$  ca. 36, which could indicate a basic number of  $x = 12$ , or perhaps dibasic with  $x = 10$  and  $x = 12$ .

Our counts for *Senecio*, one of which is reported here for the first time (*S. teretifolius*), are consistent with the previously established basic number  $x = 10$ , although Turner and Lewis (1965) report three African species with  $2n = 10$  ( $x = 5$ ). Our count of  $n =$  ca. 20 for *Pentacalia sclerosa* is consistent with previous numbers based on  $x = 10$ .

#### CICHORIOIDEAE

*Liabeae.* Our count of  $n = 9$  for *Erato sodiroi* is a new level for the species, which has been previously counted as  $n = 11$  (Strother and Panero, 1994). While our count and that of Olsen (1980) for *E. polymnioides* DC. support the suggestion by Robinson et al. (1985) that the basic number of this genus is  $x = 9$ , additional reports for *E. polymnioides* of  $n =$  ca. 11 (Sundberg & Dillon, 1986) from material taken in Huánuco, Peru, and  $2n =$  ca. 20 with possible multivalents from Ecuadorian material (Strother & Panero, 1994) could point to more complex chromosomal patterns within the genus.

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# WOOD AND BARK ANATOMY OF *NOTHOTSUGA* (PINACEAE)<sup>1</sup>

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## ABSTRACT

*Nothotsuga longibracteata* Hu ex Page is one of the rare gymnosperms endemic to China. Although previously ascribed to the genus *Tsuga*, it was recently segregated as a monotypic genus on account of its distinctive exomorphology. The wood and bark structure described here show that it has unique characteristics as well as features in common with *Tsuga*. The presence of vertical normal resin canals in the wood, together with resin cavities in the bark, does not support the earlier assignment of *Nothotsuga* to the section *Heopeuce* Keng & Keng f. of *Tsuga*, nor does it fit any other pinaceous taxon. Thus the present study supports the view that *Nothotsuga* should be validated as a genus in Pinaceae.

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*Nothotsuga* Hu ex C. N. Page is a monotypic genus and one of the rare gymnosperms endemic to China (Page, 1988). It is an evergreen forest tree up to about 30 m high, distributed in a few restricted areas of Guizhou, Hunan, Guangdong, and Fujian provinces of China (Fig. 1). With changes in the environment and ecosystems, the total number of individuals has decreased rapidly, and it is considered an endangered plant on the brink of extinction (Fu & Jin, 1992).

*Nothotsuga* was first described by Cheng (1932) as a new species in *Tsuga*. Hu (1951) placed it in a separate genus, *Nothotsuga*, on the basis of its arrangement of male strobili and the position and morphology of the female cones, which differ markedly from those in *Tsuga*. Since then, several views about its systematic position have been expressed. Gaussen (1966) treated it as a generic intermediate between *Tsuga* and *Keteleeria*, citing *Tsuga chinensis* (Franch.) Pritzl and *Keteleeria evelyniana* Masters as its likely parents. Cheng & Fu (1978) considered it to be a section under *Tsuga*. Recently, Page (1988) supplied the Latin description of the genus *Nothotsuga* to validate Hu's publication of the genus as a nomen nudum and made additional comments about the differences between *Nothotsuga* and *Tsuga*. Nevertheless, controversy still remains, since little evidence from comparative studies is available.

In this paper, the wood and bark structures of *Nothotsuga* are described in detail based on observations of both light (LM) and scanning electron microscopy (SEM), and a comparison between *Nothotsuga* and other related taxa is made in order to evaluate the systematic position and phylogenetic relationships of *Nothotsuga* in Pinaceae.

## MATERIALS AND METHODS

Wood and bark samples were obtained from two different trees grown in the subtropical region of China. The first was taken from the trunk of a living tree occurring naturally in Liancheng county of Fujian province. This sample was immediately fixed in FAA. The second, an air-dried sample from a wood disc, was obtained from the wood collection of Fujian Forestry College.

Wood samples were boiled in water and then sectioned on a sliding microtome. Bark materials were sectioned after penetration with polyethylene glycol. All sections were stained with safranin and mounted in Canada balsam. Macerations were made according to Franklin's (1945) method and mounted in glycerin jelly. Quantitative data were based on 30 measurements per sample. For SEM analysis, small blocks about 1 to 5 mm in thickness were cut off from both wood and bark samples. The transverse and radial surfaces to be observed were cleanly cut with a new razor blade. They were then soaked in a 20% solution of sodium hypochlorite until the surface lost color (Exley et al., 1977), followed by washing in running water. After dehydration through a graded alcohol series, they were mounted on stubs and coated with carbon and gold in a high vacuum evaporation unit. They were examined at 20 kV under a scanning electron microscope.

## WOOD DESCRIPTION

Growth rings are distinct with abrupt transition from earlywood to latewood. Earlywood tracheids range from 24 to 37  $\mu\text{m}$  in tangential diameter and from 0.87 to 3.6 mm in length. Tracheid cross-sec-

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